

Aggregation dynamics in juvenile queen conch (*Strombus gigas*): population structure, mortality, growth, and migration

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Abstract. Juvenile queen conch (*Strombus gigas* L.) occur in discrete aggregations within seemingly uniform seagrass beds throughout the Exuma Cays, Bahamas, suggesting that the aggregations occupy ecologically unique sectors of the habitat or that conch gain fitness by aggregated distribution. To examine the structure of a juvenile aggregation and to determine the underlying mechanisms which affect juvenile conch distribution, we examined density, size composition, growth, survivorship, and movement patterns within a typical tidal-flow field nursery over a 14 mo period (August 1989 to September 1990). At the beginning of the study in August 1989, the conch population occupied 16.7 ha, with densities >0.2 juvenile conch m^{-2} . The aggregation formed an ellipse, with longitudinal axis parallel to the main axis of the tidal current. Surveys conducted every 2 mo showed that conch density in the aggregation center remained constant while all other zones had lower densities which varied with time. In areas of high population density within the aggregation, several mass migrations of juveniles (20 to 99 conch m^{-2}) occurred in early 1990. Tagged juveniles transplanted to zones outside the aggregation had high growth rates but suffered higher losses than individuals transplanted to the aggregation center. A tethering experiment confirmed the hypothesis that predator-induced mortality is significantly higher outside than inside the conch aggregation. Our results suggest that the queen conch aggregation occupied only a portion of the habitat that is optimal for feeding and growth. Aggregations could be maintained by differential mortality over a site; however, predation rates are probably density-dependent. Gregariousness, observed in translocation experiments, may provide an active mechanism for maintaining aggregated distribution and reducing mortality in conch nurseries. The ecological significance of aggregations should be considered in fisheries management and stock enhancement programs with queen conch.

Introduction

Aggregated distributions of marine benthic fauna are observed in a vast diversity of sessile and motile taxa. Among motile invertebrates, aggregations of certain large echinoderms and molluscs have both ecological and commercial significance. Aggregations of urchins, such as *Strongylocentrotus droebachiensis* and *Diadema antillarum* have dramatic effects on macrophyte communities (Ogden et al. 1973, Bernstein et al. 1981, Carpenter 1981, Andrew 1991), and aggregations of the sea star *Acanthaster planci* are known for massive destruction of Indo-West Pacific corals (Chesher 1969). Large aggregations of scallops form the basis for commercial fisheries (Caddy 1989). Despite widespread occurrence of aggregative behavior in many large invertebrates, formation and maintenance of aggregations are poorly understood.

Queen conch (*Strombus gigas*) are large, commercially important gastropods which live as juveniles in seagrass meadows of the tropical western Atlantic (Randall 1964, Weil and Laughlin 1984). Juvenile queen conch consume little or no living seagrass, deriving most of their nutrition from macroalgae and detritus (Stoner and Waite 1991). At two nursery sites near Lee Stocking Island, Bahamas, Stoner and Waite (1990) found that juvenile conch were associated with turtlegrass (*Thalassia testudinum*) beds with intermediate biomass. They also showed that the observed distributional pattern could be due to active habitat choice.

There are vast regions of benthic habitat which appear to be appropriate for conch in terms of seagrass, detritus, sediment, and depth. Despite this, extensive surveys on the Great Bahama Bank have shown that most juvenile conch are concentrated (0.2 to 2.0 conch m^{-2}) in large aggregations (to >100 ha in surface area) in relatively few locations (Stoner and Sandt 1991, Stoner et al. 1993). In the present study, "aggregation" is defined as a large group of conch characterized by a density >0.2 individuals m^{-2} distinct over a surface area of at least several

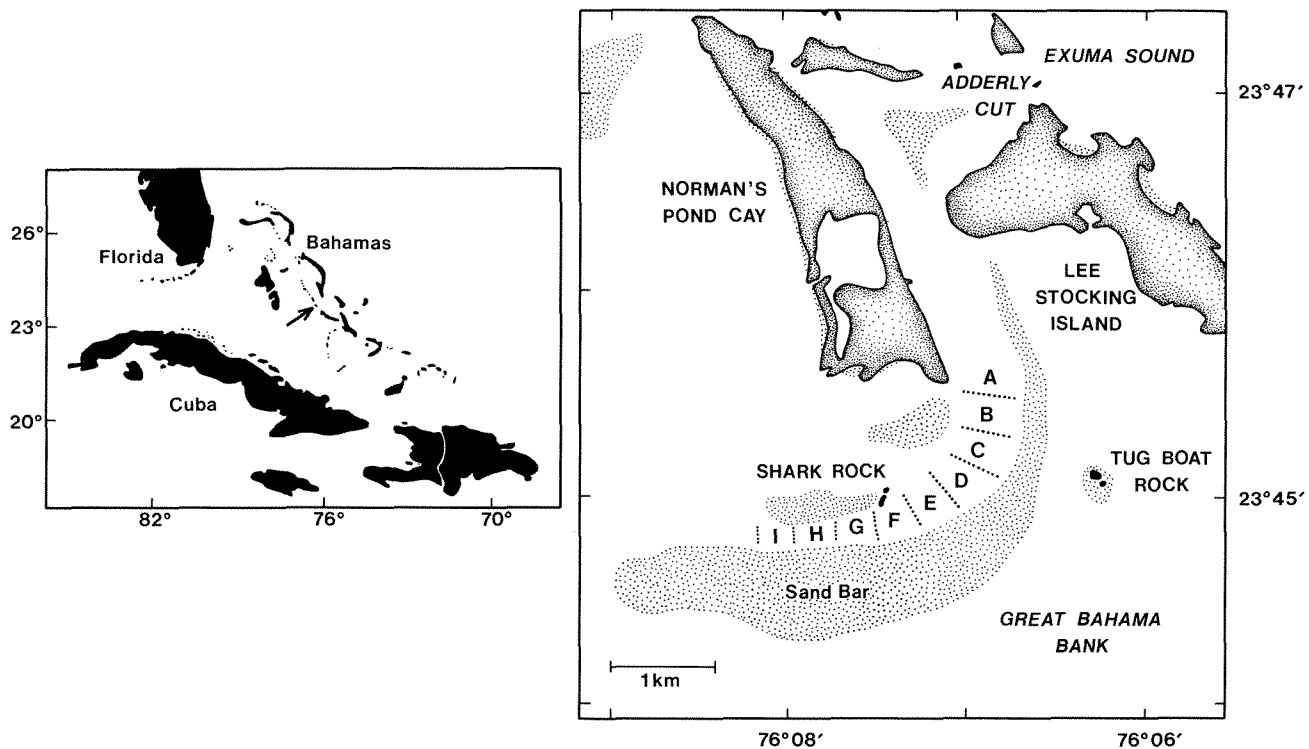


Fig. 1. Shark Rock study area comprising nine zones (A–I) within Adderly tidal flow field. Stippled areas are shallow sand < 1 m deep at mean low water

hectares. “Nursery area” is the total suitable habitat over which aggregations range in the long term.

In the Exuma Cays, Bahamas, juvenile conch aggregations occur 2.5 to 5.0 km from Exuma Sound in regions of high algal productivity (Stoner et al. 1993). Aggregations also appear to be associated with areas flushed on every tide by clean oceanic water from the Sound, and are frequently elliptical in shape with long axes parallel to tidal currents. This shape is similar to that observed in the deep-sea scallop, *Placopecten magellanicus* (Caddy 1989).

Near Lee Stocking Island in the Exuma Cays, the exact position and dimensions of any one juvenile aggregation vary over the long term; however, several aggregations have been found in the same general locations since 1984, and densities in the centers of those aggregations remain relatively constant (Wicklund et al. 1991, Stoner unpublished data). Under certain circumstances, very high-density mass migrations (20 to 200 conch m^{-2}) occur within juvenile aggregations (Stoner et al. 1988, Stoner 1989), forming groups on a smaller scale. Typically, these migrations are arranged in long (15 to 200 m), narrow (1 to 3 m) bands which lie across the axis of the tidal current and persist for several months.

The primary objective of this study was to determine how unique habitat characteristics, differential survivorship over space, and active behavioral responses affect the existence and distribution of queen conch aggregations. Measurements were made to describe the density and population structure of conch in a nursery area relative to habitat features such as depth and macrophyte biomass in a tidal flow field of the central Bahamas. Field experiments were conducted to compare growth, sur-

vivorship, and movement within and outside the peripheries of the aggregation.

Study site

The Exuma Cays are a 250 km long chain of islands on the west side of the Exuma Sound in the central Bahamas. Flood-tide waters from the Sound pass through numerous inlets between the cays onto the shallow Great Bahama Bank, where nursery grounds for queen conch are abundant in seagrass meadows (Wicklund et al. 1991, Stoner et al. 1993). This investigation was conducted on the Great Bahama Bank in the Adderly tidal flow field immediately to the west of Lee Stocking Island, near Shark Rock (Fig. 1). A large, persistent aggregation of juvenile queen conch occurs in association with this flow field near Shark Rock. This aggregation normally has an area of >10 ha and is typical of the hundreds of conch nurseries that occur in the Exuma Cays.

Drogue studies have shown that most of the flood-tide water entering Adderly Cut, north of Lee Stocking Island, advances toward Shark Rock. This primary flow field is bordered by Norman's Pond Cay and shallow, bare sand shoals to the east and south. On neap tides, water from the Exuma Sound flows west to Shark Rock, while on spring tides the tidal excursion can extend 2 or 3 km beyond Shark Rock (Stoner et al. 1993). Tidal range is ≈ 1.2 m, and reversing tidal currents frequently exceed 100 cm s^{-1} near Shark Rock. Water clarity is high, generally >15 m, except in late ebb tide during summer months.

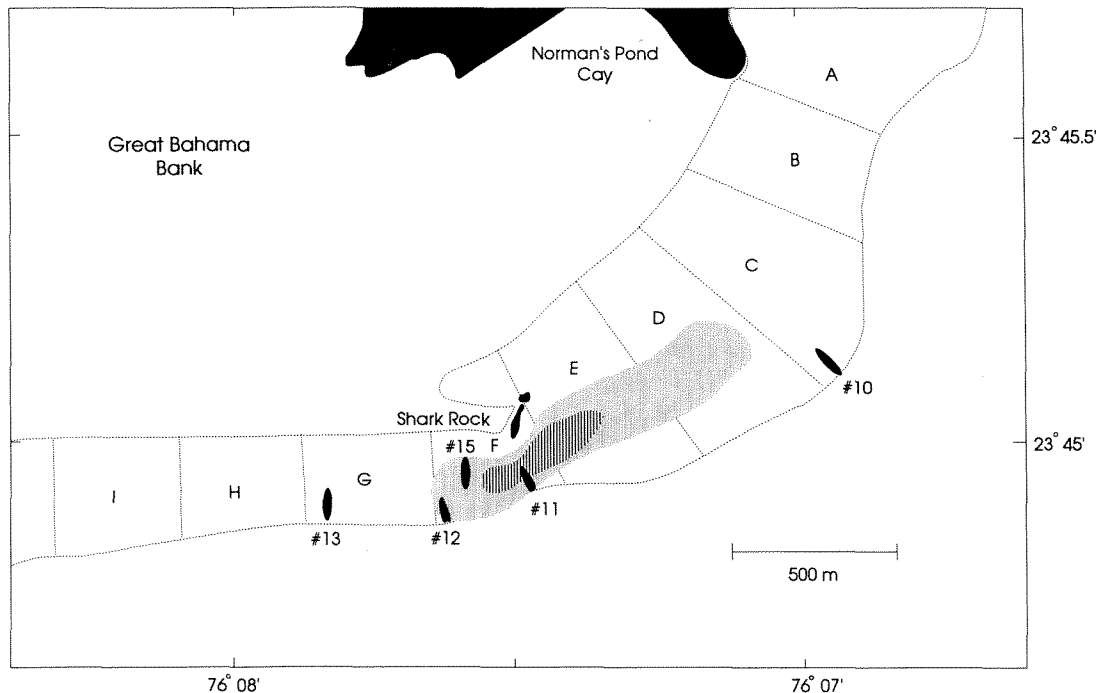


Fig. 2. *Strombus gigas*. Location of juvenile conch aggregation at Shark Rock in August 1989. Stippled and hatched areas represent areas with conch densities ≥ 0.2 and $\geq 0.5 \text{ m}^{-2}$, respectively. Locations of Mass Migrations 10, 11, 12, 13, and 15 are also shown (not drawn to scale)

Near Exuma Sound, the flow field is characterized by patchy seagrass (*Thalassia testudinum*) and algae-covered hard substrate in 5 to 8 m of water. Near the western tip of Lee Stocking Island, the bottom is characterized by large sand waves and giant stromatolites in mid-channel, and hard-bottom near the shorelines. Approximately 1.0 km from the western point of Lee Stocking Island, the bottom becomes primarily *T. testudinum*, with highest shoot density and biomass near mid-channel, grading to bare sand on both sides. During preliminary observations, few conch were found outside the seagrass area; these were primarily adults which were distributed on algae-covered hard-bottom. This investigation, therefore, concentrated on the seagrass habitat in the tidal channel.

Materials and methods

Environmental characteristics

The seagrass area of the Shark Rock tidal flow field was divided into nine arbitrary zones, each 300 m long at mid-channel and spanning the width of the channel (Fig. 1). Seagrass analysis included measurements of *Thalassia testudinum* shoot density in four replicate samples (25 × 25 cm) haphazardly placed at mid-channel in each of the nine zones. *T. testudinum* blades, living and senescent (detritus), were collected from the same quadrats, placed in 3 mm-mesh nylon bags, separated in the laboratory, and dried at 80°C for ≈ 24 h. Dry-weight biomass was standardized to g m^{-2} for the two components. Station depth was measured at low water using a weighted line marked in 10 cm intervals.

Population measurements

In the Shark Rock area, aggregations of juvenile *Strombus gigas* L. appear to have strong boundaries, where densities increase rapidly from zero. Repeated counts of the number of conch within 4 m-radius circles revealed a density of 0.2 conch m^{-2} to be typical of the periphery of the conch aggregation. In August 1989, divers were towed systematically over the study site to estimate the areal extent of the conch aggregation. Peripheries were buoyed, positions were taken using a Magellan Nav 1000 Global Positioning System, and a scale drawing of the aggregation was plotted on a small-scale topographical map. The population center was crudely estimated as the area within which conch density was $> 0.5 \text{ conch m}^{-2}$ (Fig. 2).

Density surveys were conducted every two months from September 1989 through September 1990 ($n=7$). Near the center of each zone, all conch were counted within five haphazardly-placed 4 m-radius circles, each 50.3 m^2 in area. Shell lengths (spire to siphonal canal) were measured for the first 50 conch encountered. In the zones where conch were sparse, searches were made for additional individuals to provide length-frequency data.

Juvenile conch in the Shark Rock area are frequently found migrating in densities as high as 200 conch m^{-2} . Dimensions, orientation, and persistence of the mass migrations were noted. The total length and average width of each migration was measured with a tape, and direction of movement was monitored by repeated marking of location for one week, or longer in the case of persistent migrations. Rates of progression were determined for 4 of the 5 migrations encountered during the study period. Densities were determined in a minimum of three $1 \times 1 \text{ m}$ (or larger) plots within well-defined sectors of the moving band. The total number of conch in each mass migration was estimated by extrapolating the mean density of conch over the calculated surface area of the aggregation. Shell lengths were measured for 50 to 100 individuals in four of the most persistent migrations.

Table 1. *Strombus gigas*. Initial lengths of conch (mm) from two different sources released in three zones – in outer zones of study area (B, H, I), and in aggregation center (F). Values are mean \pm SD (*n*)

Zone	Source	
	Shark Rock	Children's Bay Cay
Release 1		
B	103.0 \pm 24.8 (530)	96.6 \pm 18.8 (500)
F	103.5 \pm 23.4 (513)	101.4 \pm 17.7 (499)
I	106.8 \pm 23.0 (436)	104.9 \pm 20.7 (446)
Release 2		
B	116.0 \pm 15.7 (500)	
F	119.7 \pm 19.7 (999)	none
H	114.1 \pm 13.2 (500)	

Table 2. Depth (at low water) and seagrass (*Thalassia testudinum*) characteristics (shoot count; living, green biomass; detrital biomass) for each zone in Shark Rock study area. All seagrass values are means \pm SD (*n*=4). *F* and *p* values are for one-way ANOVA. Detritus values were log₁₀-transformed prior to analysis to improve homogeneity of variance. Means which were not different statistically are designated by the same superscripts (Tukey HSD multiple-comparison test, *p* < 0.05)

Zone	Depth (m)	Shoots (no. m ⁻²)	Green biomass (g dry wt m ⁻²)	Detritus (g dry wt m ⁻²)
A	3.4	640 \pm 22.4 ^a	60.2 \pm 11.0 ^{ab}	79.4 \pm 30.4 ^a
B	3.4	608 \pm 99.2 ^a	69.8 \pm 11.5 ^a	112.3 \pm 63.7 ^a
C	3.3	656 \pm 28.8 ^a	63.5 \pm 10.1 ^{ab}	97.0 \pm 41.0 ^a
D	3.2	512 \pm 97.6 ^a	42.6 \pm 7.8 ^{bc}	49.0 \pm 16.6 ^{ab}
E	3.2	656 \pm 65.6 ^a	62.1 \pm 9.6 ^{ab}	49.4 \pm 27.2 ^{ab}
F	3.2	576 \pm 54.4 ^a	67.5 \pm 11.2 ^a	131.5 \pm 111.8 ^a
G	2.7	496 \pm 81.6 ^a	30.7 \pm 6.9 ^{cd}	11.8 \pm 7.7 ^b
H	2.5	272 \pm 89.6 ^b	22.4 \pm 7.4 ^{cd}	8.3 \pm 5.0 ^b
I	2.5	208 \pm 35.2 ^b	16.2 \pm 3.8 ^d	6.1 \pm 2.2 ^b
		<i>F</i> = 23.0 <i>p</i> < 0.001	<i>F</i> = 20.7 <i>p</i> < 0.001	<i>F</i> = 8.7 <i>p</i> < 0.001

Tag-release studies

A tag release was conducted to determine zonal differences in growth and relative survivorship as well as movement patterns in the study area. Conch were measured and marked with colored spaghetti tags (Floy Tag and Manufacturing, Inc.) which were tied around the spire. Then tagged conch were released at two different times in three zones: the sound end of the tidal flow field (Zone B), the westernmost end (Zones H or I), and the population center (Zone F) (Fig. 1).

Conch released during 26–29 September 1989 (Release 1) were from two different sources, native individuals from Zone F of the Shark Rock site (SR) and non-natives from a nursery area near Children's Bay Cay (CBC), 5 km southeast of Shark Rock (Table 1). In exhaustive searches made by several divers drifting repeatedly in parallel lines over the zones on flood tide, these conch were recaptured and remeasured on 23–30 October 1989, 15–29 January, 14–18 April and 14 October–2 November 1990. Siphonal length and zone of recovery were recorded, and all conch were returned to the zone where found. Decreasing numbers of recovered conch could be a function of both mortality and/or emigration. Given that thorough searches were made well beyond the east and west ends of the mapped zones, and the low preference of conch for bare-sand habitat, found along the north and south borders of the study site,

the percentage of conch recovered during the four recapture periods was used as a relative index of survivorship over time and space. Spatial variation in predator-induced mortality was examined with a tether experiment (see following subsection). Mean daily rates of winter growth were calculated using up to 100 conch recaptured during the second recovery period, about 4 mo after Release 1.

To determine zonal differences in summer growth rate, a second set of native (SR) conch was released in Zones B, F, and H (Table 1) during 21–25 May 1990, and recaptured in late October. In Release 2, Zone H was used instead of Zone I because a sand bar covered portions of Zone I after Release 1. Movements and growth rates were determined as before.

Predation experiment

Tethering has been used to determine relative rates of mortality in several recent studies with juvenile queen conch (Marshall 1992, Stoner 1993). The method permits the investigator to hold test animals in specific localities and to monitor the fate of individuals. Because tethered conch have growth rates similar to those of free-ranging individuals, it has been concluded that tethering does not influence the health of juvenile conch (Marshall 1992, Stoner and Davis 1993). The method does not measure natural mortality rate, but provides data useful in comparative analysis of predator-induced mortality.

Tether experiments were conducted at the Shark Rock site in June 1991 to compare predation rates within and outside the aggregation. Tethers were placed in the center of the aggregation (Zone F), and both east (Zone B) and west (Zone G) of the aggregation. Each individual conch, similar in size (95 to 109 mm) to those tagged and released, was tied to a stainless steel welding rod with monofilament line (1 m) connected to a cable tie secured around the conch's spire. Rods were pushed into the substratum to hold the conch in place. Forty tethered conch were arranged in each of the 3 zones in 4 blocks of 10 running parallel to the axis of the tidal flow field. Mortality was monitored at 8, 16, 35, and 50 d, and shell loss or type of damage (e.g. crushed, chipped) was noted. Previous experience has shown that few conch escape from the tethering apparatus; therefore, all missing and empty or broken shells were considered to be predator-induced mortalities.

Results

Environmental characteristics

Thalassia testudinum shoot counts were similar throughout Zones A–G and lower in Zones H and I (Table 2). Living and detrital *T. testudinum* biomass was highest in Zones B and F and lowest in Zones G through I. Large variation in green biomass resulted in a high degree of statistical overlap among mean values for the nine zones. Depth decreased by about 1 m from Zones A to I.

Distribution and age structure

In August 1989, the juvenile *Strombus gigas* aggregation covered \approx 16.7 ha and extended from the east end of Zone D through Zone F (Fig. 2). Highest density (up to 1.6 conch m⁻²) occurred in Zone F throughout the study period (Fig. 3). The quantitative density survey in September 1989 indicated the presence of another group of juveniles $>$ 0.2 m⁻² in Zone B which were not present in August. This part of the aggregation expanded into Zone C in November and persisted as a secondary maximum in

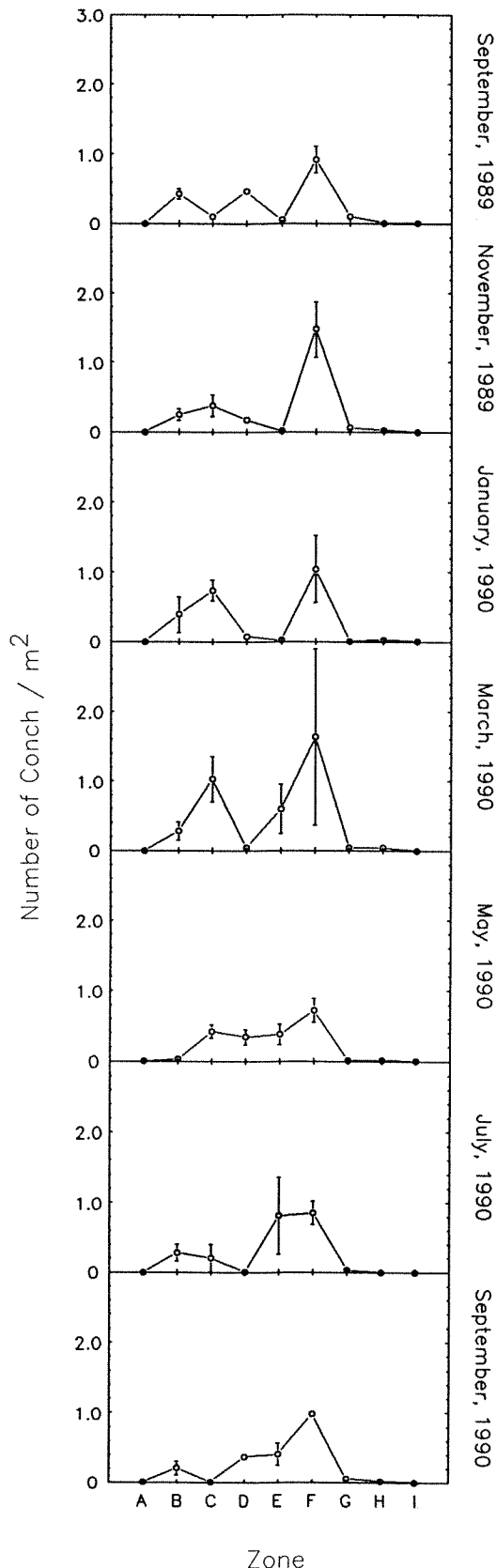


Fig. 3. *Strombus gigas*. Density of conch as a function of zone at Shark Rock during seven surveys. Values are mean \pm standard error, and are based on five samples of 50 m² each

population density over the year (Fig. 3). Adults were rare, occurring most often at the sound end of the flow field.

Conch densities were compared over space and time. Log₁₀-transformations did not improve homoscedasticity of the density data; therefore, non-parametric statistics were applied. In the seven surveys (Fig. 3), zonal differences in density were significant (Kruskal-Wallis one-way ANOVA, $p < 0.001$ in all cases). Densities in Zones C, D, E, and G changed significantly with time ($p < 0.04$ in all cases). In Zone F, however, where conch were always most dense, there was no significant change over the 14 mo study period ($p = 0.61$). Particularly high variation in conch density among March 1990 samples in Zone F was related to the presence of Mass Migration No. 11 in the zone during that time (see subsection "Mass migrations" below); 334 juvenile conch were taken within one 20 m² sample which included a section of the migration. Densities in the periphery areas, Zones A, G, H, and I, were consistently low.

Despite searches for conch outside the survey circles, length data for some zones were insufficient for length-frequency analysis; therefore, data were pooled between adjacent zones (Fig. 4). In most cases, length-frequency distributions over the flow field were unimodal. The bimodal distribution in the November survey at Zones A and B reflects the relatively high number of 2+ year-class found there. In the September 1989 survey, 1+ year-class conch (70 to 89 mm), spawned the previous summer, represented the highest proportion of all measured conch except in Zones C and D, where length-frequency was the most homogeneous (Fig. 4). Growth of this year class is demonstrated particularly well in Zones E and F, where the highest proportion of conch were 80 to 99 mm during the next three surveys. The mode was 105 mm in the May 1990 survey and 120 mm in July. By September 1990, the 1988 year-class had reached 120 to 149 mm. Growth rates indicated by changing length-frequency distributions were ≈ 0.05 mm d⁻¹ through March 1990 and 0.1 to 0.2 mm d⁻¹ through the final three surveys. These values are concordant with growth rates observed in tagged conch during the winter and summer, respectively.

Although a strong 1+ year-class was not evident in the September 1990 survey in Zones E and F, compared with the previous September, at least some <100 mm conch had emerged in all zones in March 1990 and later. These undoubtedly represent progeny from the 1989 reproductive season.

The length-frequency distribution in Zones C and D was quite different from that in the other zones. From September 1989 through March 1990 the 2+ year-class (~ 100 to 149 mm) and the 3+ year-class juveniles (> 150 mm) were well-represented. There were relatively fewer 2+ year-class conch in the other zones during these surveys except in Zones E–F in September 1990, and G–I in March 1990.

Tag recoveries

Except in the first tag recapture, conch released in Zone F were recovered at a rate at least twice as high as those

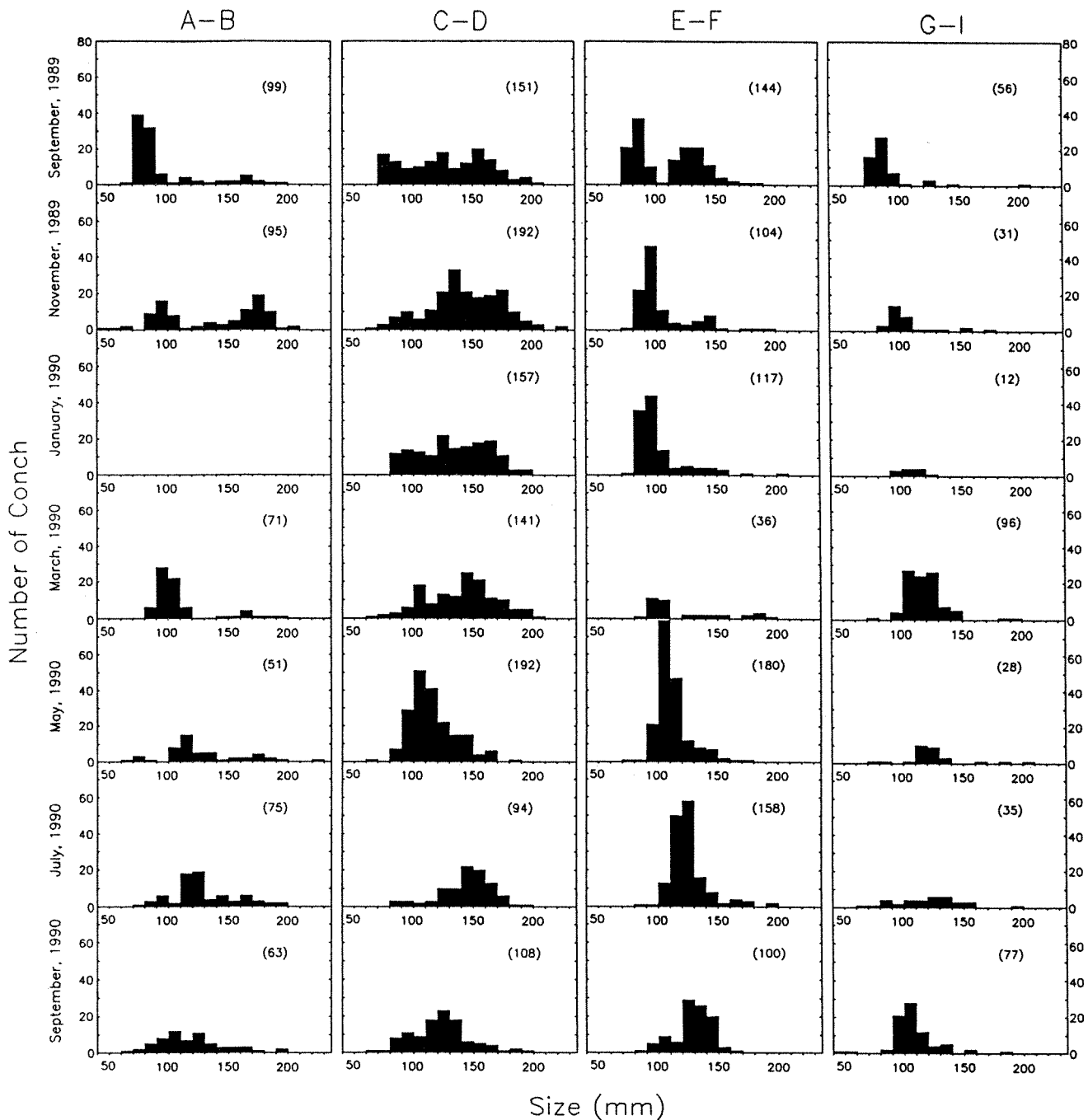


Fig. 4. *Strombus gigas*. Length-frequency distributions of all conch measured (n) in various zones of study area

released in Zones B and I (Fig. 5). Thirteen months after release, only 4% or less of the conch released in Zones B and I had been recovered, compared with 15 to 17% of those initially released in Zone F. The searches were made with as many as eight divers in very clear water on flood tide over several days, and the area was searched well beyond the zones mapped. Although not every released conch was recovered, the proportions recovered provide a good estimate of relative survivorship among the different zones.

Mean initial lengths of CBC conch released in the three zones (Table 1) were highest in Zone I and lowest in

Zone B [one-way ANOVA: $F = 25.7$, $p < 0.001$ (length values were \log_{10} -transformed to improve homogeneity)]. Despite a potential size advantage over the smaller conch in terms of susceptibility to predators (Appeldoorn 1984), few of the larger CBC conch released in Zone I were recovered alive. Mean initial lengths for SR conch (Release 1) were not significantly different.

Decreasing numbers of tagged conch recovered in the peripheral zones could have been a function of high mortality and/or movement toward the aggregation. Movements were shown by records of the location of tagged conch (Fig. 6). Conch released in Zone B tended either to

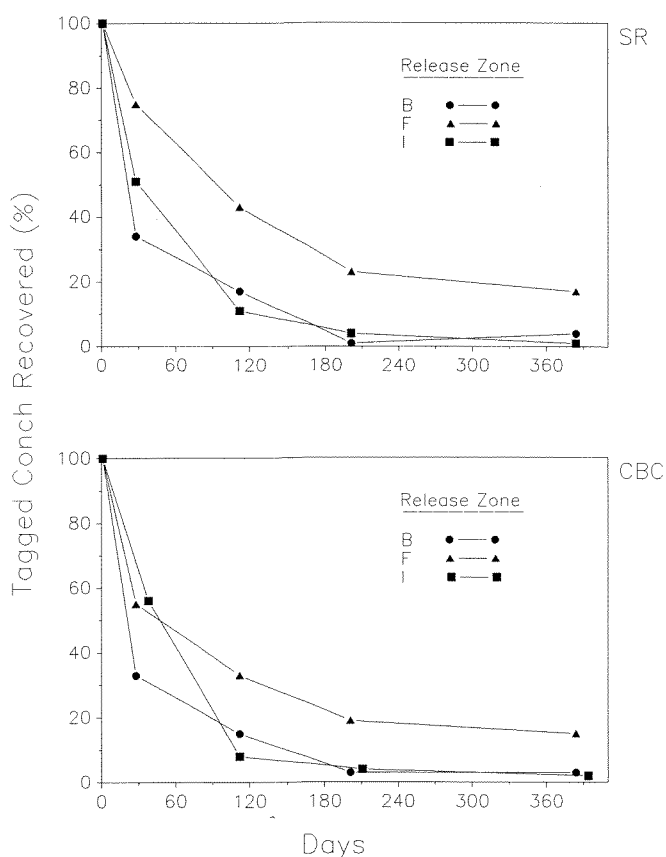


Fig. 5. *Strombus gigas*. Percentage of conch recovered following releases in three different zones in Shark Rock nursery area. Zone F was inside juvenile aggregation, other zones were outside. SR: native individuals from Shark Rock; CBC: non-natives from nursery area near Children's Bay Cays

stay there or move towards the aggregation. Conch released in Zone I moved furthest. Although only 2% of the conch released in Zone I had been recovered at the end of the experiment, all of these conch were found within the aggregation in Zone F, and none were found in Zone I. Those released in the aggregation (Zone F) tended to remain there and were rarely recovered beyond Zones E and G. There were no marked differences between the movement patterns of native SR conch and non-native CBC conch (Fig. 6).

Predation in different zones

The predation rate on tethered conch was strongly influenced by location (Fig. 7), with relatively few conch killed (18%) inside the juvenile aggregation (Zone F), and all 40 conch tethered in Zone B killed by Day 35. On Day 8, the proportion of conch killed was significantly greatest in Zone B and lowest in Zone F (ANOVA: arcsine-transformed data, variances were homogeneous, $F=20.01$, $p<0.001$; Tukey; $p<0.03$ for all 3 pairwise comparisons). By Day 50, 57% of the conch tethered just outside the juvenile aggregation (Zone G) had been killed, and the mortality rate in Zone G continued to be significantly

Table 3. *Strombus gigas*. Results of pairwise analysis of covariance for growth rates of juvenile conch in three different zones within study site, with initial shell length as covariate. Where slopes for the two zones were heterogeneous, F values for test of slope are shown. Values for n are numbers of individual measurements for growth rate

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>	<i>n</i>
Release 1 – SR conch					
Zones B vs F	1	0.052	114.64	<0.001	B = 90
Covariate	1	0.007	14.60	<0.001	F = 100
Error	187	0.000			I = 46
Zones B vs I	heterogeneous slopes, $F=56.60$, $p<0.001$				
Zones F vs I	heterogeneous slopes, $F=67.12$, $p<0.001$				
Release 1 – CBC conch					
Zones B vs F	1	0.078	124.38	<0.001	B = 75
Covariate	1	0.013	21.35	<0.001	F = 100
Error	172	0.001			I = 36
Zones B vs I	1	0.028	30.86	<0.001	
Covariate	1	0.022	24.14	<0.001	
Error	108	0.001			
Zones F vs I	heterogeneous slopes, $F=7.39$, $p<0.007$				
Release 2 – SR conch					
Zones B vs F	1	0.003	3.20	0.075	B = 100
Covariate	1	0.006	7.78	0.006	F = 100
Error	197	0.001			H = 100
Zones B vs H	1	0.019	21.20	<0.001	
Covariate	1	0.012	13.27	<0.001	
Error	197	0.001			
Zones F vs H	1	0.007	8.64	0.004	
Covariate	1	0.008	10.12	0.002	
Error	197	0.001			

greater than that in Zone F (variances were homogeneous, Student's t -test, $t=-3.91$, $p=0.008$).

Growth rates in different zones

Growth rates of free-ranging, tagged conch in the three different release zones were compared using analysis of covariance (ANCOVA) with length as the covariate because of weak negative correlations between growth rate and initial conch length (Fig. 8). Because of heterogeneous slopes in growth rates among the three zones for individuals from both SR and CBC in Release 1, pairwise comparisons were made (Table 3). Despite a lack of homogeneity in slopes for growth rates in SR conch in Release 1, juveniles outside the aggregation (Zone B) grew at rates significantly higher than those inside the aggregation (Table 3). At 100 mm standard length (SL), growth rates of SR and CBC were nearly identical (Fig. 8). For CBC conch in Zones F and I, regression-line slopes for growth rates were heterogeneous; however, it is clear from the pairwise ANCOVAs that growth rates decreased significantly from Zones I to B to F. At 100 mm SL, near the mean size of conch released in Experiment 1, conch in the aggregation center (Zone F) grew at 0.06 mm d^{-1} ,

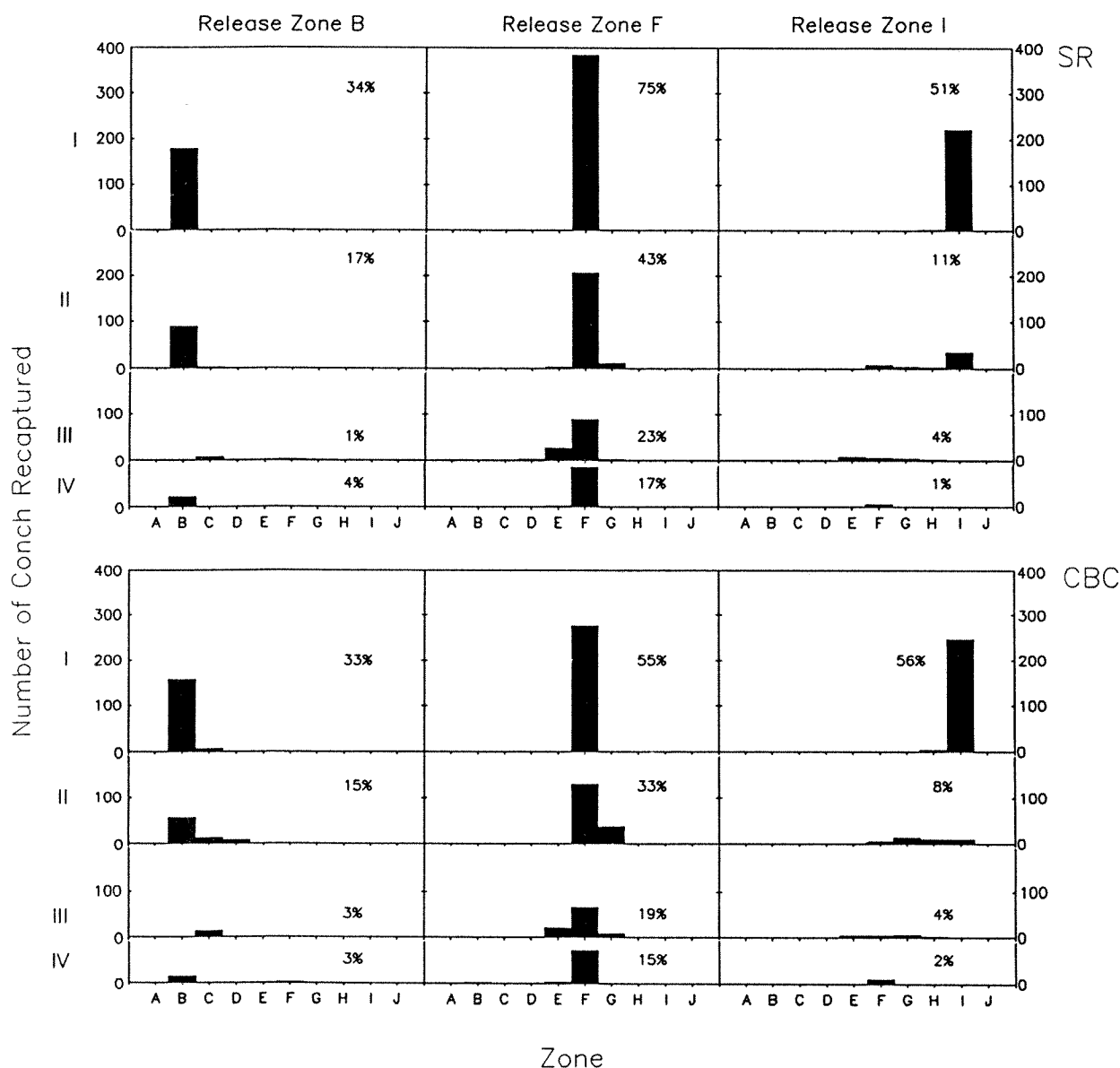


Fig. 6. *Strombus gigas*. Number of live conch collected from two different sources (SR and CBC) which were released in three zones in September 1989 and recaptured during four recovery periods (I, October 1989; II, January 1990; III, April 1990; IV, October

1990). "J" is included in the recovery zones merely to show lack of conch recovered west of Zone I; it is not one of the nine zones considered quantitatively in this study. Living conch recovered during each recapture are reported as percent of initial number released

while conch outside the aggregation in Zones I and B grew approximately twice as fast (0.14 and 0.11 mm d^{-1} , respectively).

Predictably, summer growth rates, measured in Release 2, were generally higher than those observed in the winter (Fig. 8). The regression lines for growth rates in the second experiment did not have different slopes ($F=0.643$, $p=0.526$), and zone effects were less than those in Release 1. For example, there was no significant difference in growth rates between Zones B and F (Table 3), where growth rates of 100 mm conch were $\approx 0.15 \text{ mm d}^{-1}$.

In conclusion, growth rates of free-ranging tagged juvenile conch outside the aggregation were as high or higher than those observed in the aggregation center,

with maximum differences in the winter. Areas outside the aggregation appear to provide satisfactory habitats for the nutritional requirements of the conch.

Mass migrations

Five mass migrations of juvenile queen conch were observed in the Shark Rock area during the study period (Table 4). All the migrations involved high-density groups of juvenile conch arranged in long narrow bands which lay across the tidal current (perpendicular to the axis of the flow field) (Fig. 2). Four of the migrations were present in December 1989 through January 1990.

Migration #10¹ was first observed in Zone C in late October (Fig. 2) and persisted for 3.5 mo. This migration was composed of ≈ 2600 large juveniles (mean shell length = 148 mm), similar to those in Zones C and D in January (Fig. 4). This band of juvenile conch advanced west, in the direction of the flood tide, at $\approx 2.5 \text{ m d}^{-1}$.

The largest migration (#11) was first observed in late December 1989, in Zone F. Although the dimensions of this migration were not large, density was high (99 conch m^{-2}), and the calculated total number of conch in the migration was over 12 000. This mass migration was comprised of relatively small conch which averaged 107 mm (Table 4) and were similar in size to the surrounding conch in Zones E and F (Fig. 4). Migration #11 was the most persistent migration and the most dynamic in terms of motion. The migration progressed toward the west (flood-tide direction) at $\approx 2.9 \text{ m d}^{-1}$ for the first three months of observation, then reversed direction to advance toward the east approximately one month before it dispersed, in mid-April 1990. Reversal of direction and dispersion appeared to be related to movement of the conch into and around an area which contained high densities of foods interspersed with the seagrass habitat. The green alga *Batophora oerstedii* was particularly abundant and is known to be a preferred food item (Stoner unpublished data).

Migration #12, in Zone F, involved ≈ 6300 individuals arranged in a long (100 m), narrow (1.5 m) band. This migration persisted for three months and moved in the direction of the flood tide at 2.3 m d^{-1} .

Migration #13 and 15 were both small (<30 m in length; Table 4). The density of conch in Migration #13 was relatively low (22 conch m^{-2}) and involved <1000 conch. This migration was well defined for less than one

¹ Migration numbers are applied chronologically in a long-term analysis of mass migration in the vicinity of Lee Stocking Island (Stoner and Lally 1993). Because many migrations have been found outside the Shark Rock nursery, migration numbers start at 10 and are not sequential.

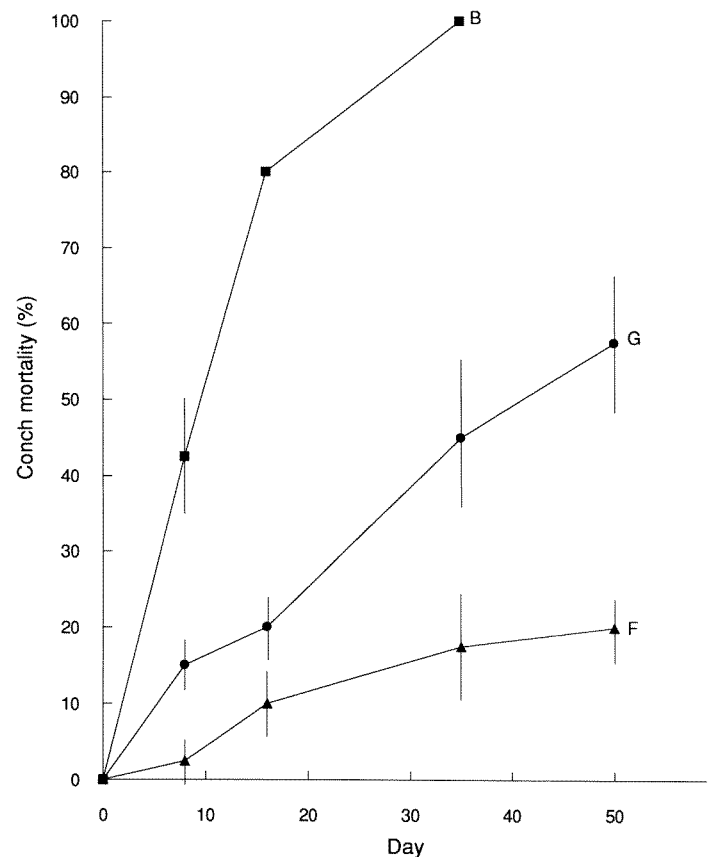


Fig. 7. *Strombus gigas*. Percentage of conch killed per block of tethers in Zones B, F, and G of Shark Rock nursery area. Zone F was inside juvenile aggregation, and Zones B and G outside. Values are mean \pm standard deviation error

month in December and January. A large number of conch were observed in the relatively short Migration #15 because of high width (2.5 m) and density (95 conch m^{-2}). For two months, this migration moved eastward, toward the Exuma Sound, at a rate of $\approx 2.4 \text{ m d}^{-1}$. Mean conch length (140 mm) was similar to that observed in

Table 4. *Strombus gigas*. Dimensions, density and movements of five mass migrations of queen conch near Shark Rock, Lee Stocking Island, Bahamas, 1989–1990. Direction of movement indicates progression of migrations in direction of ebb or flood tidal currents. Total number of conch is extrapolated from density and dimensions. Values are mean \pm SD. nd: no data

	Mass Migration No.				
	10	11	12	13	15
First observation	25 Oct. 1989	21 Dec. 1989	21 Dec. 1989	21 Dec. 1989	23. Oct. 1990
Last observation	8 Feb. 1990	14 Apr. 1990	16 Mar. 1990	22 Jan. 1990	24 Dec. 1990
Direction of movement	flood	flood to ebb 03-12-90	flood	flood	ebb
Length of mass migration (m)	60	65	100	29	28
Width of mass migration (m)	2.2 ± 0.6	1.9 ± 0.3	1.5 ± 0.3	1.5 ± 0.4	2.5 ± 0.2
Density (no. m^{-2})	20 ± 2	99 ± 17	42 ± 10	22 ± 8	95.6
Total no. of conch	2 640	12 226	6 300	957	6 650
Mean shell length mm (n)	148 ± 22 (50)	107 ± 24 (80)	nd	nd	140 ± 10 (100)

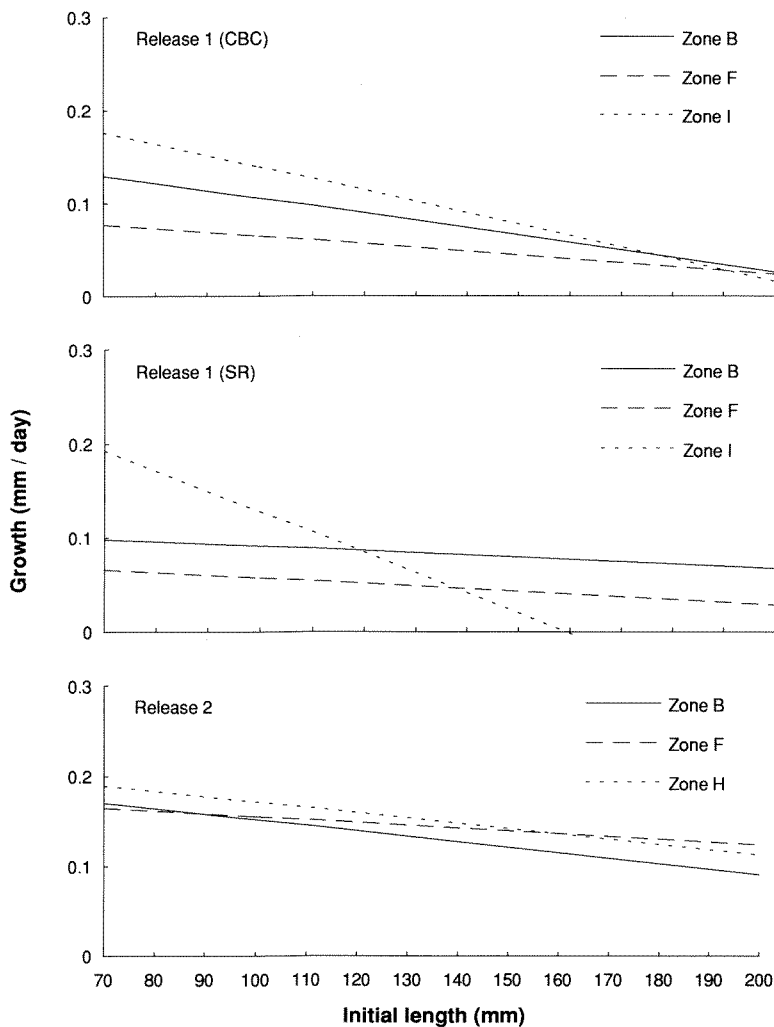


Fig. 8. *Strombus gigas*. Regression lines for relationship between conch length and growth rate in three different zones of Shark Rock nursery area. Release 1 represents winter period during which juvenile conch from two different sources (SR and CBC) were observed for growth. Release 2 was conducted in summer with SR conch only. Zone F was inside, Zones B, H, and I outside juvenile aggregation

Zones E and F in September 1990 and probably represents the same year-class as the smaller conch observed earlier in Migration #11.

To estimate the numerical significance of conch in mass migrations within the Shark Rock juvenile aggregation, the total number of conch in migrations was compared with the extrapolated total number for dispersed conch in January and September 1990. The number for the overall aggregation was calculated from the mean density of conch for each zone multiplied by the length of the zone (300 m at mid-channel) and by the approximate width of the zone defined as the portion covered with moderate density seagrass and known to have resident conch. In January 1990, the total population in the nursery ground was $\approx 162\,000$ conch, 13.6% of which were in Mass Migrations 10, 11, 12, and 13. In September 1990, the total population had declined to $\approx 105\,000$ conch. In October, $\approx 6.4\%$ of the total population was in Mass Migration #15.

Discussion

The association of juvenile *Strombus gigas* with seagrass meadows is well established. The densities of 0.2 to 2.0 juvenile conch m^{-2} found in this study are similar to

those in other conch nurseries in the Bahamas, Cuba, Turks and Caicos Islands, Venezuela, and Virgin Islands (Randall 1964, Alcolado 1976, Hesse 1979, Weil and Laughlin 1984, Iversen et al. 1987). Persistent juvenile aggregations located within larger, seemingly uniform seagrass beds, could be explained by one or more of at least four possible mechanisms: (1) Particular habitat characteristics make the site of aggregation ecologically unique, (2) settlement of larvae is contagious, (3) aggregations occur as a function of differential post-settlement survivorship (predation), and/or (4) juvenile conch are gregarious.

Large-scale distribution of juvenile queen conch is related to seagrass shoot density in the Exuma Cays, Bahamas (Stoner et al. 1993), and field experiments have shown that this correlation could be a function of active habitat choice (Stoner and Waite 1990). The position of the conch aggregation near Shark Rock, however, was independent of shoot density. Although shoot and conch density were both low in the westernmost zones (H and I), only conch density was low in Zones A and B, while seagrass characteristics were similar to those in the population center (Zone F).

Given that certain macroalgae and epiphytes are important sources of carbon for juvenile conch rather than

live seagrasses (Randall 1964, Stoner and Waite 1991), it is plausible that abundance of conch may be more closely associated with biomass or productivity of algae, and other important environmental variables cannot be ruled out as determinants of juvenile conch distribution. The transplant experiments conducted in this study, however, show that growth rates of conch outside the aggregation were equal to or higher than rates inside the aggregation, and it is unlikely that the dimensions of the observed aggregation are defined by habitat. Furthermore, low growth rates inside the aggregation were probably density-dependent. Winter growth rates, which were higher outside the aggregation than inside, suggest that reduced winter production of algal foods may be limiting to conch in high-density areas. However, the fact that the nursery site was not "saturated" implies that the aggregation was recruitment-limited through either the supply of larvae or post-settlement survivorship.

Caddy (1989) suggested that elliptical aggregations of *Placopecten magellanicus* orientied along a tidal axis could be formed by swarms of competent larvae being transported tidally and settling to the benthos over a relatively short period of time. This does not seem a plausible explanation for the formation of juvenile conch aggregations. Queen conch near Lee Stocking Island have a long reproductive season (April to October), and larvae are abundant in the water column for several months (Stoner et al. 1992). Larvae appear to be somewhat concentrated over known nursery sites near Lee Stocking Island, but veliger densities are typically low, and swarms of larvae have not been observed in 4 yr of plankton sampling (own unpublished data). In addition, recent experiments have shown that queen conch do not settle gregariously or preferentially with conspecifics (Davis and Stoner 1993).

Low tag-returns of free-ranging conch and high mortality of tethered conch outside the aggregation suggest that maintenance of the Shark Rock aggregation was related to predation. Two explanations for high survivorship in the population center are plausible: First, low mortality in the aggregation could be a function of low predator density within the central nursery area. Aronson (1989) has shown that high-density beds of ophiuroids are often associated with sites and periods of low predator abundance. Given that juvenile conch aggregate in the middle of relatively uniform habitats and the fact that most of their predators are large and motile (e.g. sting rays, spiny lobster, hermit crabs, and predaceous snails such as *Fasciolaria tulipa*), it is unlikely that conch aggregations are formed in areas of low predator abundance. Surveys of predators such as these are difficult because of their high motility or cryptic nature, and have not been conducted. A more likely mechanism for aggregation maintenance is density-dependent refuge for juvenile conch provided by the aggregation. Field experiments with juvenile queen conch have shown that predation risk to individuals declines with conch density (Marshall 1992), and aggregations of juveniles may be maintained by active behavioral mechanism. New experiments will be needed to examine interactions between the habitat, predator density, and conch mortality and density.

Gregariousness in juvenile *Strombus gigas* is suggested by the fact that tagged conch (even non-native individuals) moved toward the aggregation from two different locations outside the aggregation, while tagged individuals released within the aggregation tended to remain. Scheibling (1985) observed a similar gregarious response in sea stars (*Oreaster reticulatus*) translocated from aggregations. Although mechanisms of orientation are unknown, Scheibling concluded that gregarious behavior kept the sea stars in preferred patches of food. Conspecific attraction in *Acanthaster planci* was attributed to detection of feeding activity (Ormond et al. 1973). A similar proximal mechanism could occur whereby algal pigments released by large, feeding aggregations of conch, carried on tidal currents, serve as attractants to other conch. Ultimately, however, we hypothesize that gregariousness in juvenile queen conch is an evolved behavior, whereby predation rates are reduced by aggregation. Winter growth data showed that conch within the aggregation were nutritionally disadvantaged, but this state was compensated by higher survivorship.

Intraspecific sociability in juvenile queen conch is further suggested by the presence of high-density mass migrations within the nursery area. Wave-like migrations of juvenile *Strombus gigas* have been known since Stoner et al. (1988) reported a persistent high-density migration of over 100 000 juveniles in the Exuma Cays in 1987 (Stoner and Lally 1993). Migrations observed in the present study were relatively small, with dimensions, densities, and composition similar to a migration observed in 1988 (Stoner 1989). The mechanisms involved in mass migration are still unknown, although two lines of evidence suggest that the initiation of mass migration is density-dependent. First, the highest incidence of mass migration was recorded during November 1989 through March 1990, when densities in Zone F were > 1.0 conch m^{-2} . Second, in experiments where the density of conch in large enclosures was manipulated (0.5 and 5.0 conch m^{-2}), a tendency to migrate in an oriented fashion was observed at densities > 2.0 conch m^{-2} (own unpublished data). Given that mass migration may be an important aspect of aggregation dynamics in productive nursery grounds, and that similar migrations are observed in other invertebrates (Lowe and Turner 1976, Bernstein et al. 1981, Scheibling 1985), further investigation is warranted.

Data from the present study, along with a growing body of literature (review by Stoner et al. 1993), suggest that the large-scale boundaries of nurseries for queen conch are set by specific physical and biological conditions such as circulation, depth, seagrass shoot density, and food production provided in unique sectors of large seagrass meadows. The structure of the aggregations, however, appears to be maintained by predation and/or intraspecific attraction, perhaps evolved as a response to predation. Catterall and Poiner (1983) concluded that mixed age-class "colonies" of *Strombus luhuanus* were organized in a similar manner, but they emphasized the role of gregariousness. New experiments should be designed to separate the direct and indirect effects of predation.

Over the last 25 yr, the release of hatchery-reared juvenile queen conch has been frequently suggested as a viable mode for rehabilitation of seriously overfished stocks in the Caribbean region (Berg 1976, Ballantine and Appeldoorn 1983, Laughlin and Weil 1983, Davis et al. 1985, Berg and Olsen 1989, Stoner 1993). However, both fisheries management and hatchery-based stock-enhancement programs must be based on an understanding of the mechanisms underlying the distribution of the species. Juvenile aggregations and the nursery habitats they occupy must be identified and protected – they are vitally important in the population dynamics and healthy fisheries of queen conch.

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